EARLY CRETACEOUS POLAR TETRAPODS FROM THE GREAT SOUTHERN RIFT VALLEY, SOUHTEASTERN AUSTRALIA

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Early Cretaceous deposits from southeastern Australia record a cold, extensively forested environment. Tetrapod fossils in channel fills, gravity flows, lag and point bar dcposits in the Aptian Wonthaggi and Albian Middle Eumeralla formations. The fossils occur mainly in horizontally-stratified, clast-supported conglomerates and massive, matrix-supported conglomerates. Leaf mats indicate that several species of deciduous plants shed their leaves together, presumably in winter. Taphonomy of the lake beds at Koonwarra indicatc seasonal freezing. A varicty of dinosaurs — including hypsilophodonts, ankylosaurs, neoceratopsians, allosaurs, dromaeosaurs, oviraptorosaurs and ornithomimosaurs — were prescnt as well as pterosaurs, plesiosaurs, temnospondyls and crocodilians. The latter two groups did not occur together and the temnospondyls lived under either cooler or higher-energy conditions than the crocodilians. ☐ *Cretaceous, Australia, dinosaur, environment of deposition, palaeoclimate, temnospondyl.*

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Breakup of Gondwana began in the Late Triassic. Australia and Antarctica were the last two continents of the supercontinent to separate, commencing in the Late Jurassic. During the Early Cretaceous, betwecn 125 and 105 million years ago, what is now the southern coast of Victoria, Australia, was part of a rift valley formed between the two continents during the initial phase of that separation. As separation continued and sped up, the floor of the rift valley sank. As a consequence of that event, volcanoes that probably lay near the Lord Howe Rise, poured quantities of ash (estimated at 50,000 cubic kilometres) into the rift valley where it was then reworked by the rivers and streams, the precursors to the green sandstones and mudstones that now form prominent cliffs for about 200km of the Victorian coastline (Fig. 1).

Since that rift valley was formed, Australia has drifted far to the north, while Antarctica remained close to its Early Cretaceous position straddling the South Pole. In the Early Cretaceous southeastern Australia lay well within the Antarctic Circle. The dinosaurs, other fauna and plants that lived in this region thus contended with prolonged periods of continuous darkness each year, just as musk ox and reindeer do today. However, the geochemical and botanical climatic indicators suggest that the environment in the Early Cretaceous of Victoria was not frigid as are similar latitudes today, and extensive forests clothed many parts of the rift valley and its flanks at times.

ENVIRONMENTAL SETTING OF THE TETRAPOD FAUNA

A small, but growing, collection of fossil tetrapods are known from several locales in southeastern Australia (Currie, Vickers-Rich & Rich, 1996; Gross, Rich & Vickers-Rich, 1993; Molnar, Flannery & Rich, 1981; 1985; Rich & Rich, 1989; Rich & Vickers-Rich, 1994; Rich et al., 1988; 1992; Vickers-Rich & Rich, 1993; Warren et al., 1991). These fossils have been collected from three geologic units: 1, the younger Middle Eumeralla Formation of Early Albian age in the Otway Group; 2, the older undifferentiated Wonthaggi Formation of Aptian age in the Strzelecki Group; and 3, the Aptian San Remo Member near the base of the Wonthaggi Formation.

Fossils are concentrated in a few facies within these units: i.e., 1, mainly those preserved as a consequence of rapid deposition in a new channel cut as a consequence of a single major flood; 2, as gravity flows of sediment, either mud or rock debris; and to a lesser extent, 3, lag and point bar deposits within major river systems (A. Constantine, pers. comm.).

The bones are most commonly preserved in horizontally stratified, clast-supported conglomerates and massive, matrix-supported conglomerates. A 'clast-supported conglomerate' refers to one in which the individual pebbles or boulders contact one another, whereas a 'matrix-supported conglomerate' is one in which the quantity of finegrained rock between the pebbles or boulders is so great that they do not contact one another. If the matrix could be removed from a clast-supported conglomerate, the volume occupied by the conglomerate would not decrease, whereas in the case of a matrix-supported conglomerate, it would.

The horizontally stratified, clast-supported conglomerates are typically of the order of 5-20cm thick and are characterised by pebble to cobble-sized clasts formed of clay and mudstone. Such deposits are stratified and contain little carbonaceous material. This type of bone-bearing conglomerate typically occurs at the base of channel complexes where significant erosion into underlying floodplain claystones and mudstones is evident. Such deposits are interpreted as having formed by streams or rivers breaking their banks during major floods, with the resultant flood waters flowing out over the surrounding floodplain, picking up bones and plant debris and concentrating them in erosion scours.

The massive, matrix-supported conglomerates, on the other hand, differ in that the pebble to boulder-sized clasts are not touching each other. Instead, they appear to be suspended in a finer-grained matrix composed of fine to medium-grained sandstone. Mudstone is again the dominant clast type, and plant remains are not as common. Conglomerates of this type are interpreted as debris flows, which form as the result of bank collapses within the confines of channels.

The regional setting for the two geological units that have produced significant fossil collections shows distinct change through time, from a predominantly 'meandering' to a 'braided' system upsequence. The older Wonthaggi Formation is characterised by thick floodplain deposits and channels with moderate to high sinuosity. There are thick accumulations of horizontally stratified to low angle crossbedded sediments, which indicate rapid aggradation under transitional to high flow regimes — suggestive of occasional flash flooding. The formation consists of about 60% sandstone and 40% mudstone and reflects varying flow regimes, perhaps due to discharge levels controlled by snow melt. Vertebrate fossils have been recovered from a variety of lithofacies within the formation, but mainly from horizontally stratified, clast-supported conglomerates and massive, matrix-supported conglomerates.

The younger Middle Eumeralla Formation consists primarily of sandstone (more than 70%) and is characterised by a classic braided river lithofacies and architecture. Sinuosity of channel deposits is low, and the channels were wide and shallow. There are thick sequences of both floodplain and lacustrine sediments with lenses of sand-sized particles representing individual channels stacked one on top of another. Vertebrates occur in only a few environmental settings, somewhat in contrast to the situation in the Wonthaggi Formation — in the Middle Eumeralla bones occur predominantly in sediments formed when a channel broke its bank and flowed out over the surrounding floodplain, or in those formed by loading and collapse of non-vegetated sand bars in the main channel during a peak flood stage that caused liquefaction of sand and then down-slope mass flow.

THE BIOTA: PALAEOFLORA AND INVERTEBRATE FAUNA AS PALAEOCLIMATIC INDICATORS

The palaeoflora of southeastern Australia during the Early Cretaceous was dominated by conifers, ferns, cycads, ginkgoes and lower-growing horsetails and bryophytes. Angiosperms were present, but only as prostrate or small herbaceous forms. The structure and diversity of this flora suggest a mean annual temperature of 8-10°C (Douglas, 1969; 1971; Drinnan & Chambers, 1986; Parrish et al., 1991). Some plants in this flora were evergreens, while others were clearly deciduous, the best evidence being fossilised leaf mats suggestive of simultaneous shedding of leaves by several species. The evergreen plants possessed leaves with thick cuticle and microphyllus (small) leaves. Such leaf morphology is consistent with a climate characterised by significant variation in temperature throughout the year or a fluctuating water supply — conditions that would be expected within a continental land mass distant from the ocean. Leaf mats themselves are indicative of leaves having fallen in a short period of time — which can be brought on by pronounced seasonal changes in light, temperature or water availability or a combination of these factors. Pronounced seasonal contrasts are expected of such inland environments at such latitudes as was the case in southern Victoria in the Early Cretaceous (Parrish et al., 1991).

One unusual locality to have produced fossil plants, invertebrates, fishes and birds, is Koonwarra. Koonwarra is an inland site in the Won-

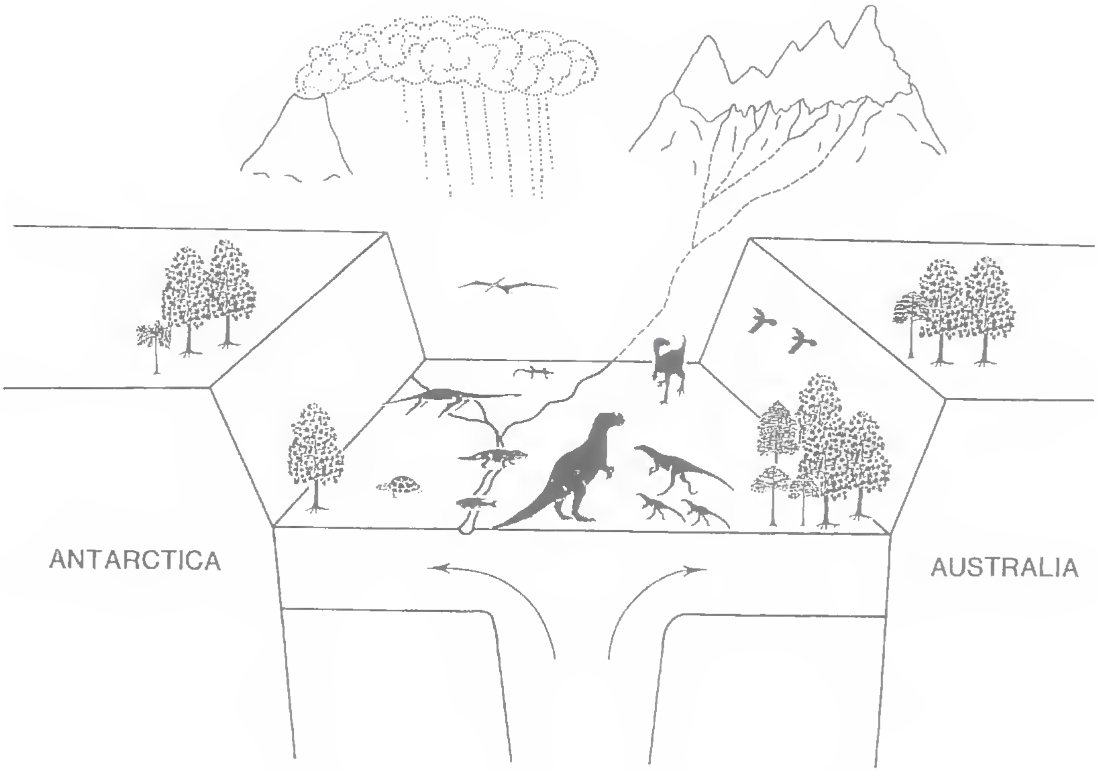

FIG. 1. Sketch of junction between SE Australia and E Antarctica in the Early Cretaceous. Separation began in the Late Jurassic and resulted in a rift valley being formed on the interplate boundary. Into this rift valley poured a vast quantity of volanogenic sediments derived from volcanoes perhaps laying to the east in the vicinity of the Lord Howe Rise. Large rivers flowed across the floor of this rift valley, fed perhaps in part by meltwater of snow presumably located at high altitude on mountains on the margins of the rift valley or the volcanoes which produced the volcanogenic sediments. The Early Cretaceous tetrapod and plant fossils occur for the most part in sediments that were laid down in small streams feeding into the larger rivers on the floor of the rift valley. Subsequent to the Early Cretaceous, the sediments deposited on the floor of the rift valley were first lithified as they were buried under additional sediment. Then late in the Cainozoic, these sediments were uplifted to form the Strzlecki and Otway Ranges.

thaggi Formation of the Strzelecki Group and represents the remains of an ancient lake. Most other vertebrate sites in southeastern Victoria are coastal exposures, and fossils were deposited not in the quiet waters of large lakes, but in the more energetic riverine and floodplain environments. Insects and other invertebrates, primarily larval forms, recovered from the Koonwarra locality are most closely related to forms typical of cool Tasmanian mountain lakes today (Jell & Duncan, 1986), relationships that are indicative of temperatures similar to those reflected by the palaeoflora. Waldman (1971), who studied the Koonwarra fish concentration, suggested that the entire fossil accumulation may have been due to winterkill — when the lake froze over and oxygen supply was greatly reduced.

Further evidence that temperatures were cool and that ice may have formed at times during the year occurs in contemporaneous sequences in central Australia. Boulders up to 3m in diameter have been found in otherwise finegrained marine sediments of the Bulldog Shale near Andamooka, South Australia (Frakes & Francis, 1988). Frakes & Francis have suggested that these boulders dropped to the bottom of the shallow sea as icebergs in which they floated, melted away. Although there is no preserved evidence — such as tillites — for glacial activity in Australia at this time, unlike for the earlier Permian time, Frakes has suggested that montane glaciation could have been active and, in places, these glaciers might have reached the sea at the base of drainage systems.

In summary, the suite of animals, plants and sedimentological data suggest that the climate of southeastern Australia during the late Early Cretaceous when dinosaurs are known to have lived there, was somewhat cooler than at present, but temperatures were by no means frigid as similar high polar latitudes are today. O^{18}/O^{16} evidence, however, suggests that mean annual temperatures approached 0°C at times during deposition of the dinosaur-bearing sediments.

VERTEBRATE ASSEMBLAGES OF THE EARLY CRETACEOUS OF POLAR AUSTRALIA

The Early Cretaceous terrestrial vertebrate assemblages of southeastern Australia are dominated by dinosaurs, in particular hypsilophodontids. There are at least five genera and six species of this family known from Victoria, half as yet unnamed. The diversity of hypsilophodontids in these south polar latitudes is unmatched anywhere else in the world, including localites with hundreds of thousands of bones and high diversity in the total dinosaur assemblage. Currie (pers. comm.) has suggested that at lower palaeolatitudes, hypsilophodontids may have been upland forms and thus not frequently represented at the lower elevations where most dinosaur fossils accumulated. Hypsilophodontids, then, may well have been preadapted for the conditions of southeastern Australia and consequently thrived there. Hyspilophodonts are known from both the Otway and Strzelecki Groups and thus have an age range in these sequences from Aptian to Albian, with some sites perhaps being as old as Valanginian in the Strzelecki Group.

On the basis of femoral morphology, five genra of hypsilophodontids have been recognised. To date, formal scientific names have been assigned to only three of these: *Fulgurotherium*, *Leaellynasaura* and *Atlascopcosaurus*. Prominent optic lobes preserved on an endocast of *Leaellynasaura* suggest that this dinosaur had unusually enhanced ability to process visual signals. In a polar setting, the most plausible explanation for this acuity would be that it improved visual ability under the low light conditions, which would have prevailed during the months of continuous darkness of the polar Winter. Since both palaeobotanical and geochemical studies suggest that Winter temperatures would have probably dipped below freezing, and since this is a prohibitive temperature for activity of modern reptiles, it is tantalising to think that *Leaellynasaura* may have been homeothermic — thus allowing the increased visual acuity to have an adaptive advantage.

Other ornithischians in the fauna include an ankylosaur (based on the cross-sectional outline of a rib, a scute and a few teeth) and an Aptian neoceratopsian (based on an ulna with a remarkable resemblance to that of *Leptoceratops gracilis* from the latest Cretaceous of Alberta).

Allosaurids, oviraptorosaurs and ornithomimid theropods are known. An astragalus resembling that of *Allosaurus* has been recognised in the Aptian Wonthaggi Formation of the Strzelecki Group (Molnar, Flannery & Rich, 1981; 1985). Oviraptorosaurs (Currie, Vickers-Rich & Rich, 1996) and ornithomimids (Rich & Vickers-Rich, 1993) are both known from the Middle Eumeralla Formation in the Otway Group, and ornithomimids have also been recovered from the older Strzelecki Group (Wonthaggi Formation). Footprints of small theropods have been recorded in the Otway Group.

The neoceratopsian, dromaeosaur and oviraptorosaur fossils from Australia are among the oldest records of these groups anywhere in the world. Other components of the fauna include the young temnospondyl amphibians, which are represented by more than twenty bones, including a pair of mandibles with the teeth in situ. Two bones of pterosaurs and half a dozen plesiosaur teeth have also been recovered. Evidently the plesiosaurs were freshwater animals, as all sedimentological and palaeontological data point to a fluviatile source for the containing sediments.

A few remains of crocodiles have been recovered in the Middle Eumeralla Formation in the Otway Group, but never have they been found together with temnospondyl remains, restricted as they are to the older Strzelecki Group. A warming trend up section in the Aptian-Albian sequence may explain this apparent faunal change — the replacement of temnospondyls by crocodiles.

The Victorian Aptian record of temnospondyls is the most recent for the group anywhere in the world. These amphibians were very crocodile-like functionally — in body form and in tooth morphology. Temnospondyls occur in the older Aptian sediments where temperatures were lower than in the younger Albian sediments that bear a few dermal scutes of crocodiles. Perhaps the rising temperatures allowed the invasion of crocodilians into an area from which they had been excluded by the cold waters, thus bringing them into direct competition with the temnospondyls, followed by extinction of the latter. Today amphibians, such as frogs and the Giant Japanese Salamanders are able to cope with temperatures well below those tolerated by living reptiles.

The evidence is suggestive, but not definitive, however, for there is one other possible explanation that cannot be ruled out. Temnospondyl fossils are known from the Strzelecki Group only in the high energy sediments that represent fanglomerates pouring off the margins of the rift valley. This coarse facies occurs widely in the western exposures of the Aptian Strzelecki Group, but is less common in the younger Aptian Otway Group. Perhaps temnospondyls were facies controlled, and thus their absence is owing to sparsity of the coarse fanglomerate facies in the younger sediments of the Otway Group, rather than their extinction by the Albian owing to temperature increase or some other factor.

CONCLUSION

Although genera endemic to southeastern Australia occur in these Early Cretaceous assemblages, there is nothing yet recognised as unique as the modern day koala or kangaroo. All of the tetrapods found to date can be readily accommodated in families known from other continents. But what is clear is that in the Early Cretaceous, southern Australia served as a refuge allowing some groups to live well beyond their time elsewhere in the world (e.g., *Allosaurus,* temnospondyls and some fish and plant groups). This area also nurtured novelty — it may have been the cradle for such groups as the neoceratopsians, dromaeosaurs and oviraptorosaurs — a cradle from which they dispersed later, northwards, to meet with great success in North America and Asia.

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